senting cells. Contributions from Gleichmann’s laboratory have provided another dimension for this approach by examining lymphoproliferative responses to different xenobiotics in vivo. This work complements our studies because it demonstrated that immune reactivity was not against the administered compound, but a metabolite of higher oxidation state; we showed how such products could be produced within a lymphoid compartment.

In order to account for the autoimmune side effects of drugs, Gleichmann and colleagues adopt a variant of the conventional explanation of drug-altered self-proteins as the initiating event. Other recent proposals include direct activation of lymphocytes through redox cycling or inhibition of DNA methylation reactions. However, the features of drug-induced lupus and the nature of SLE suggest that ultimate understanding might require an explanation for which there is currently no precedent.

Robert L. Rubin
W. M. Keck Autoimmune Disease Center, Department of Molecular and Experimental Medicine, The Scripps Research Institute, 10666 North Torrey Pines Road, La Jolla, CA 92037, USA

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Thumbs, Tools, and Early Humans

By comparative functional analysis of thumb morphology, the report by Randall L. Susman (1) tackles the key question of which extinct hominids used tools. He contrasts living apes and their short, thin, weak thumbs and resultind power grasps with living humans and their long, stout, strong thumbs and refined precision grasps. The latter is said in the report to be correlated with tool behavior of extinct hominids; it is proposed, for example, that Australopithecus afarensis with its ape-like thumb was not a toolmaker, but Paranthropus robustus with its human-like thumb was.

Even with their inferior thumbs, however, apes engage in dextrous manipulation of objects by precision grasping and make and use a variety of tools (2). Most of these tools are made from vegetation and so will not endure in any future archaeological record, but this is beside the point. Some of the tools of wild chimpanzees are of stone and show characteristic wear patterns (3). To deny tool behavior to hominids older than 3 million years ago on the basis of their ape-like thumbs is thus unfounded. One could say that a particular kind of hominid technology, flaked stone, has not yet been seen in wild apes, although it has been shown in captive ones (4). More fruitful might be detailed studies of living apes and humans in terms of which types of grasps are associated with which types of tool-useing and -making, especially in terms of task demands and raw materials.

W. C. McGrew
Department of Sociology and Anthropology and Department of Zoology, Miami University, Oxford, OH 45056, USA

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Randall L. Susman (1) makes a significant contribution toward our understanding the appearance of toolmaking capabilities in early hominids. He (1) proposes a test that “relies on a single thumb element and one that is well represented in the fossil record” to “help resolve the question of which Pliocene hominids were responsible for the earliest tool assemblages” (1, p. 1572).

The inference of behavior from morphology in fossil taxa is warranted if (i) there is some living species that bears the morphological trait, (ii) the trait is used for the same behavior in all living taxa that possess it, (iii) there is a clear functional linkage between the behavior and the trait, and (iv) there is no evidence that the trait arose in the living species before the behavior was adopted (2). Given these rules of comparative analysis, we reassess the evidence presented by Susman (1) for tool use among fossil hominids with the use of our data on gorilla thumb morphology.

Susman (1) describes several thumb muscles present in humans, but absent in apes, which he states are required for using a precision grasp. Noting that large transarticular forces are produced at the human metacarpocephalgeal joint by these muscles, Susman (1) explains the relatively expanded human metacarpal head as an adaptation to reduce joint stress. He concludes that “humans have broader metacarpal heads than apes” (1, p. 1571) and, using a ratio of metacarpal head breadth to metacarpal length, shows that “values for African apes and modern humans do not overlap” (1, p. 1571). Susman (1) then uses this ratio as a criterion to separate modern toolmakers from non-toolmakers and to infer toolmaking capabilities in fossil hominids.

We tested this hypothesis by measuring pollical metacarpal head breadth and metacarpal length in adult humans, bonobos, and chimpanzees, and expanded the sample to include gorillas (3). When these data are plotted along with those of adult humans, following Susman (1), metacarpal head breadth of gorillas exceeds that of chimpanzees and overlaps markedly the range of variation shown for humans (Fig. 1A). Applying the ratio used by Susman (1), the range of values for mountain gorillas overlaps that of humans more than it does that of chimpanzees (Fig. 1B). The majority of fossil taxa for which tool use is implied by Susman (1) fall well within the range of variation observed for gorillas (Fig. 1B) (4). Susman also noted “great apes have relatively shorter thumbs than do humans, with metacarpals that are reduced in relative length” (1, p. 1571). Plots of thumb metacarpal length against body size (3 in adult apes and humans demonstrate that, at comparable body sizes, adult gorillas have first metacarpals that do not differ significantly in length from those of humans (6).

The presence of a wide metacarpal head relative to metacarpal length is proposed by Susman (1) as a reliable test for human-like precision grasping and tool use in fossil hominids. However, gorillas possess a wide metacarpal head (Fig. 1), but do not use a precision grip and do not manufacture stone tools. Thus, not all living taxa which possess the trait use it for the same behavior, (contrary to i). Our results (6) also demonstrate that the proposed (1) functional link between metacarpal length and precision grasping is problematic. The gorilla-human pattern could be interpreted as primitive for African apes and humans, with Pan possessing the derived (6) morphology as a specialization for arboreal life. Thus (iv) is also violated in light of evidence suggesting the metacarpal proportions of Homo sapiens could have evolved before the adoption of tool use.

These conclusions then beg the question of what might be a robust morphological correlate of precision grasping and tool use in fossil hominids. As Napier (7) noted, “precision grip . . . is not an essential requisite at this [Oldowan] level of craftsman-
Thumbs, tools, and early humans
MW Hamrick and SE Inouye

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